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被子植物镜像花柱及其进化意义

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Enantiostyly in angiosperms and its evolutionary significance

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Abstract Enantiostyly, deflection of style to left or to right side of floral axis, is a kind of style polymorphism. Based on organization of left- and right-styled flowers present on individual plants, enantiostyly can be expressed as two quite distinct forms: monomorphic and dimorphic enantiostyly. In monomorphic enantiostyly, individual plants produce both floral forms, either mixed within an inflorescence or segregated between left- and right-styled inflorescences, and this condition is not a genetic polymorphism. In dimorphic enantiostyly, plants are exclusively left- and right-styled, and this condition is a genetic polymorphism. Based on patterns of arrangement of style and stamens in individual flowers, enantiostyly can be expressed as reciprocal and nonreciprocal enantiostyly. Reciprocal enantiostyly is commonly associated with the reciprocal deflection of a pollinating anther, but in nonreciprocal enantiostyly there are no pollinating anther deflections. Enantiostyly has been reported in 11 families of angiosperm. It is generally considered to play an important role in (1) protecting the functional pistil and stamens, (2) insuring reproduction by selfing, and (3) increasing male fitness and outcrossing rates by reducing sexual interference between female and male function. Enantiostyly has been hotly-debated in plant reproductive biology. The purpose of this paper is to review and analyze recent advances in enantiostyly research, with emphases on 1) types of enantiostyly and morphological differentiation and floral characteristics of mirror-image flowers; 2) taxonomy, genetics and evolution of angiosperms that exhibit enantiostyly; and 3) the evolutionary biology of mating patterns and pollinating characteristics associated with enantiostyly. Finally, prospects for further research in this area are discussed. Our review provides a database for further study of the evolutionary biology of enantiostylous species and points out the significance of enantiostyly in the evolution of breeding systems of plants.

Key words angiosperms, breeding system, enantiostyly, evolution.

摘要 镜像花柱是指花柱在花水平面上向左(左花柱型)或向右(右花柱型)偏离花中轴线，是一种花柱多态现象，可根据左、右花柱花在植株上的排列式样划分为单型镜像花柱和二型镜像花柱两类，或根据镜像花柱和雄蕊的排列方式划分为雌雄互补镜像花柱和非雌雄互补镜像花柱两类。镜像花柱现象已在被子植物11个科的部分种类中进行了报道，它在保护功能型雄蕊和雌蕊、通过自交产生繁殖保障效应以及通过减小雌雄功能间干扰、提高异交率和雄性适合度等方面具有重要的进化意义，目前已成为植物繁殖生物学领域的研究热点。本文总结分析了国际上有关镜像花柱的研究工作，重点介绍: (1)镜像花柱

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的类型、镜像花的形态分化及花部特征, (2)镜像花柱植物在被子植物中的分布及其遗传演化, (3)镜像花的交配式样和交配频率、传粉特点及其进化生物学意义, 并对今后的研究方向进行了展望, 以期为进一步研究镜像花柱植物的进化生物学特性, 推动我国在该领域的发展提供科学依据。
关键词 被子植物; 繁育系统; 镜像花柱; 进化

镜像花柱(enantiostyly)这一术语最早为Knuth (1906)第一次使用, 是指花柱在花水平面上向左(左花柱型)或向右(右花柱型)偏离花中轴线(Barrett et al., 2000)。具有镜像花柱的花称为镜像花(mirror-image flowers), 它是由Todd (1882)在观察到黄花刺茄*Solanum rostratum* Dunal.和*Chamaecrista fasciculata* (Michx.) Greene (又名*Cassia fasciculata* Michx.或*C. chamaecrista* L.)植株的同一花序中同时存在左花柱花(left-styled flowers)和右花柱花(right-styled flowers)时第一次报道。Wilson (1887)也观察到在*Wachendorfia paniculata* L.居群中同时出现左、右花柱植株的现象。随后, 不少学者也相继报道了该现象(Iyengar, 1923; Bowers, 1975; Ornduff & Dulberger, 1978; Dulberger & Ornduff, 1980; Dulberger, 1981; Webb & Lloyd, 1986)。镜像花柱作为一种典型的花柱多态现象, 在保护植物功能型雄蕊和雌蕊以及通过减小雌雄功能间干扰来促进异花传粉等方面具有重要的进化意义(Dulberger, 1981; Jesson, 2002; Jesson & Barrett, 2002b, 2003, 2005)。因此, 对镜像花柱的研究已成为近年来国际上植物繁殖生物学领域的一个新的生长点(Dulberger, 1981; Jesson, 2002; Jesson & Barrett, 2002b, 2003, 2005; Tang & Huang, 2005; Gao et al., 2006)。

目前, 国际上对植物镜像花柱现象的研究主要集中在对镜像花的形态特征与花器官发生(Jesson et al., 2003b)、镜像花柱植物的分布与遗传演化(Barrett et al., 2000; Barrett, 2002b; Jesson & Barrett, 2003)、镜像花的传粉特点(Bowers, 1975; Ornduff & Dulberger, 1978; Dulberger, 1981; Jesson & Barrett, 2002c; Tang & Huang, 2005; Gao et al., 2006)、镜像花柱植物的交配式样及其进化意义(Dulberger, 1981; Jesson, 2002; Jesson & Barrett, 2002b, 2003, 2005)等方面。

中国是世界上被子植物物种多样性最丰富的国家之一(宋延龄等, 1998), 众多的植物类群及其千姿百态的花部式样以及复杂的地形地貌, 是研究植物繁殖生物学的“天然实验室和材料基地”。在这些“基地”中, 可能存在着不少鲜为人知的、具镜像花柱的植物类群, 这些将为我们研究植物繁育系统的进化提供丰富的实验材料。但我国对植物镜像花柱现象的研究近两年才刚刚起步, 已有的报道仅限于对少数类群的花展示及其传粉生物学特性的研究(Tang & Huang, 2005; Gao et al., 2006)。有鉴于此, 本文在前人工作的基础上全面分析与总结了镜像花柱的类型、镜像花的形态分化及花部特征、镜像花柱植物在被子植物中的分布及其遗传演化, 分析并讨论了镜像花的交配式样和交配频率、传粉特性及其可能的进化生物学意义。同时对今后的研究方向进行了展望, 以期为进一步研究镜像花柱植物的进化生物学特性, 推动我国在该领域的发展提供科学依据。

1 镜像花柱的类型、镜像花的形态分化及花部特征

1.1 镜像花柱的类型

镜像花柱可划分为以下几种类型: 一是根据左、右花柱花在植株上的排列式样将其

划分为单型镜像花柱(monomorphic enantiostyly)和二型镜像花柱(dimorphic enantiostyly)两类；二是根据镜像花柱和雄蕊的排列方式将其划分为雌雄互补镜像花柱(reciprocal enantiostyly)和非雌雄互补镜像花柱(nonreciprocal enantiostyly)两类(Jesson & Barrett, 2003)。

单型镜像花柱是指左、右花柱花呈现在同一植株上。居群是单型的，所有植株具有相同的花表现型，不是遗传多态现象(图1: A)(Fenster, 1995; Graham & Barrett, 1995; Wang et al., 1995)。该类又可分为两个亚类：一是镜像花柱展现在同一花序上(即花序上同时具左、右花柱花)，如在雨久花科Pontederiaceae的*Monochoria korsakowii* Regel & Maack和茄科Solanaceae的黄花刺茄等植物中；另一是镜像花柱分别展现在同一植株的不同花序上，如雨久花科的*M. australasica* Ridl. (Jesson & Barrett, 2003)。单型镜像花柱植物左、右花柱花在花序上的排列呈现出有规则、花柱偏向可预测和不规则、花柱偏向不可预测两种式样，如在黄花刺茄等植物中，只要花序上第一朵花的花柱偏转确定，那么其他花的花柱偏向完全可被预测，而在*Cyanella lutea* L. f.和*M. korsakowii*等植物中，左、右花柱花在花序上的排列是随机的，其花柱偏向也是随机不可预测的(Jesson et al., 2003b)。二型镜像花柱是指居群内个体表现为左、右花柱植株(图1: B)，植株上花柱偏向固定，是一种真正的遗传多态现象，如在雨久花科的*Heteranthera multiflora* (Griseb.) Horn等植物中(Jesson & Barrett, 2002b, 2003)。二型镜像花柱植物左、右花柱花在花序上的排列是单一的(Knuth, 1906)。但*C. alba* L. f.在温室中仅10%的植株表现为单型镜像花柱(Dulberger & Ornduff, 1980)，而在南非Wuppertal的较大居群中大部分植株同时产生左、右花柱花，表现为单型镜像花柱，说明该植物具不完全二型镜像花柱(Jesson & Barrett, 2003)。

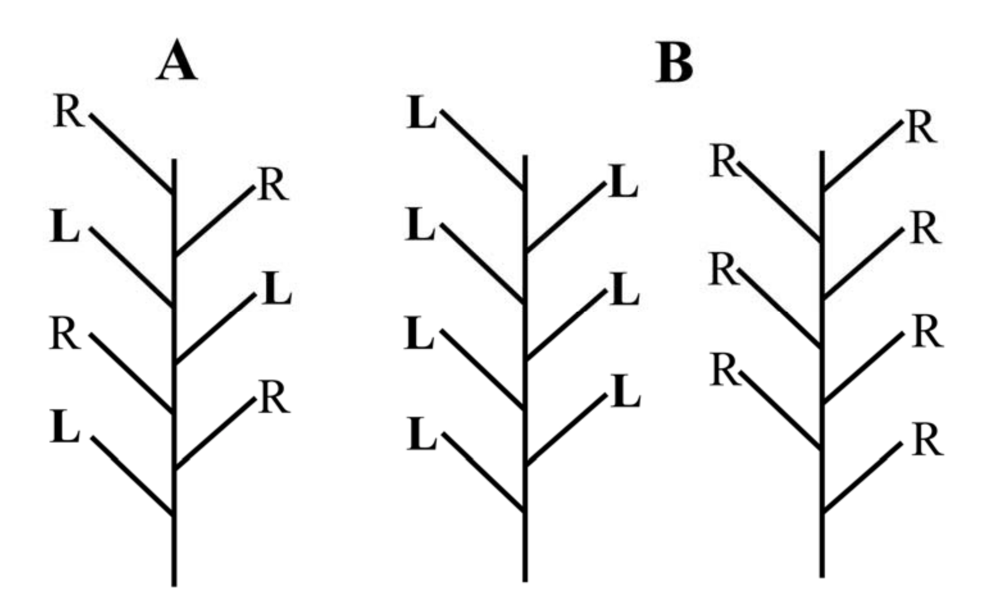


图1 镜像花柱的类型 A，单型镜像花柱；B，二型镜像花柱；L，左花柱型花；R，右花柱型花 (引自Barrett et al., 2000)。

Fig. 1. The types of enantiostyly. A, monomorphic enantiostyly; B, dimorphic enantiostyly; L, left styled flowers; R, right styled flowers (from Barrett et al., 2000).

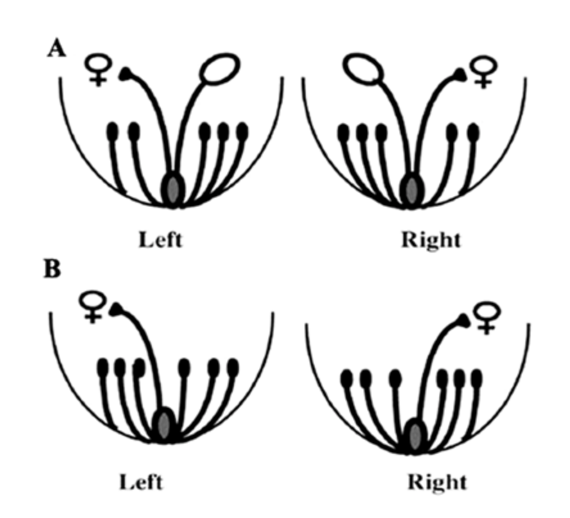


图2 镜像花柱的类型 A, 雌雄互补镜像花柱; B, 非雌雄互补镜像花柱(引自Jesson & Barrett, 2003)。
Fig. 2. The types of enantiostyly. A, reciprocal enantiostyly; B, nonreciprocal enantiostyly (from Jesson & Barrett, 2003).

雌雄互补镜像花柱是指镜像花内花柱偏转通常与1枚或2枚雄蕊偏转方向相反(图2: A), 这枚雄蕊的花药比其他雄蕊的稍大, 颜色较暗且与传粉相关, 称为传粉花药(pollinating anther), 而其余颜色亮丽、不发生弯曲的花药主要是吸引传粉昆虫并为其提供食物, 称为喂饲花药(feeding anther)。二型镜像花柱通常属于雌雄互补镜像花柱(Jesson & Barrett, 2003)。非雌雄互补镜像花柱指镜像花内花柱偏转方向与雄蕊偏转方向无关, 且雄蕊功能无差异(图2: B), 如苦苣苔科Gesneriaceae的非洲紫罗兰 *Saintpaulia ionantha* Wendl. 等植物(Knuth, 1906; Simpson, 1990; Lloyd & Webb, 1992; Evans et al., 2000; Jesson et al., 2003b)。

另外, 有些植物所有植株的花柱偏转方向相同, 如在南非好望角*Tenicroa exuviata* (Jacq.) Speta (百合科Liliaceae)的5个居群中, 所有植株都具有右花柱花且花柱偏离雄蕊, 但这不是镜像花柱, 只是代表了异型花的一种类型(Jesson & Barrett, 2003)。

1.2 镜像花的形态分化

目前, 对镜像花的形态分化研究主要集中在雄蕊群与雌蕊群的分化以及花型间左右不对称性的分化两方面。

1.2.1 雄蕊群与雌蕊群的分化 Jesson等(2003b)在对黄花刺茄等9种镜像花柱植物观察后认为, 不同类群镜像花柱植物雄蕊群的发生与分化均先于雌蕊群, 传粉雄蕊先于喂饲雄蕊形成, 但在雄蕊群的形态分化与长度、传粉花药发生弯曲的时间以及花柱发生弯曲的时间上均存在着差异。从雄蕊群的功能分化看, 二型镜像花柱植物花内雄蕊群的花药通常分化为传粉花药和喂饲花药, 而单型镜像花柱植物则表现出3种分化式样: 有传粉花药和喂饲花药的分化(如黄花刺茄)、无传粉花药和喂饲花药的分化(如*M. australasica*)或花内仅有一枚雄蕊(如田葱*Philydrum lanuginosum* Gaertn.)。从雄蕊长度看, 二型镜像花柱植物传粉雄蕊与喂饲雄蕊的长度无明显差异, 而单型镜像花柱植物某些种的传粉雄蕊和喂饲雄蕊长度不同(如*Dilatris corymbosa* Bergius、*H. limosa* Willd.、*H. rotundifolia* Griseb.、*Cyanella lutea*和黄花刺茄), 这些差异不是生长速率的差别, 而是由于花丝或花药发育的起始和终止时间不同造成的。正是由于传粉雄蕊与喂饲雄蕊长度的不同使得它们的功能也不相同(Endress, 1999; Jesson et al., 2003b)。从传粉雄蕊发生弯曲的时间看, 单型镜像花柱植物传粉雄蕊表现为开花前发生弯曲(如黄花刺茄)或开花前6–12 h发生弯曲(如*M. hastata* (L.) Solms和*M. vaginalis* (Burm. Fil.) Kunth), 而二型镜像花柱植物传粉雄蕊发生弯曲的时间未见报道。从花柱发生弯曲的时间看, 一些二型镜像花柱植物花柱发生弯曲的时间与单型镜像花柱植物花柱发生弯曲的时间类似, 表现为花柱于花蕾长到5–7

mm (发育完全状态的25%–45%)时发生弯曲(如*D. corymbosa*、田葱和*W. paniculata*)，或开花前或开花时发生弯曲(如*C. lutea*、*H. limosa*、*H. multiflora*、*H. rotundifolia*、*M. australasica*和黄花刺茄)，但少数单型镜像花柱植物花柱于开花前6–12 h发生弯曲(如*M. hastate*和复总望江南*Cassia didymobotrya* Fresen.)(Iyengar, 1923; Dulberger, 1981; Jesson et al., 2003b)。因此，Jesson等(2003b)认为，花蕾的空间局限性可能是导致花柱弯曲表达比较晚的因素之一。

1.2.2　花型间左右不对称性的分化　不同类群镜像花柱植物花型间左右不对称性的分化具有差异。如在二型镜像花柱植物*H. multiflora*中，当传粉雄蕊和雌蕊发育高度相同时(即花发育晚期)，柱头表面长出乳头状小突起且发育不规则，花柱偏离传粉雄蕊，若花柱偏左，传粉雄蕊则偏右，反之亦然，由此发生左右不对称性的分化; *H. multiflora*较大花蕾的柱头发育也具明显不对称性，开花前24 h柱头相对于花序轴向左或向右发生偏转，且柱头的偏向通常与花柱的偏向相反。单型镜像花柱植物*H. limosa*左右不对称性的分化与*H. multiflora*类似，只是花柱弯曲比后者发生得早(Jesson et al., 2003b)。Iyengar (1923)在*Monochoria* Presl中发现，单型镜像花柱植物*M. hastata*和*M. vaginalis*所有雄蕊的花丝上都有1–2个长度不等的刺，大刺通常位于传粉雄蕊花丝上，雄蕊发生弯曲前这些刺不等长，可作为左右不对称性发生的早期标志；而*M. australasica*不具传粉雄蕊，花丝上也没有刺。因此，比较该属种间的花发育也许能揭示不对称性在发生时间上的差异。但无论是单型镜像花柱还是二型镜像花柱植物，花型间的左右不对称性都在花发育的晚期发生分化(Tucker, 1999; Jesson et al., 2003b)。

1.3　镜像花的花部特征

镜像花柱植物有着多样化的花部特征，主要表现在花对称性、花瓣联合程度、雄蕊群特征、雄蕊群与花柱间的关系及花柱特征等方面。

从花对称性看，单型镜像花柱植物镜像花的花瓣表现出辐射对称(如*D. corymbosa*和*H. limosa*，图3: A，C)、轻微两侧对称(如黄花刺茄，图3: E)及明显两侧对称(如田葱和*C. lutea*，图3: F，G) 3种式样；二型镜像花柱植物镜像花的花瓣仅表现出辐射对称(如*M. australasica*，图3: B)和轻微两侧对称(如*W. paniculata*，图3: D) 2种式样(Jesson & Barrett, 2003)。

从花瓣联合程度看，单型镜像花柱植物镜像花的花瓣表现出离生(如*D. corymbosa*和*C. lutea*)、基部合生(如*H. limosa*、*H. rotundifolia*和*M. australasica*)、基部与小苞片融合(如田葱)及基部与花萼融合(如黄花刺茄) 4种式样，而二型镜像花柱植物镜像花的花瓣仅表现出基部合生(如*H. multiflora*和*W. paniculata*)(Jesson et al., 2003b)。

从雄蕊群特征看，不同类群镜像花柱植物的雄蕊在数目、形态与着生位置及偏转方向上均存在差异(附录1；图3)。有些单型镜像花柱植物花间或花内雄蕊间花粉特征存在差异，如复总望江南花中3组可育雄蕊每雄蕊内的花粉数具明显差异，2枚最大可育雄蕊的花粉数是其他5枚可育雄蕊花粉数的3.7倍以上，位于最下方中间的1枚可育雄蕊花粉数最少，最大可育雄蕊的花粉粒比其他可育雄蕊的稍小，传粉花药和喂饲花药花粉败育率无差异(Dulberger, 1981); *C. lutea*传粉花药中的花粉数多于每一枚喂饲花药的花粉数(Dulberger & Ornduff, 1980)。黄花刺茄花内传粉花药的花粉数是喂饲花药平均花粉数的2

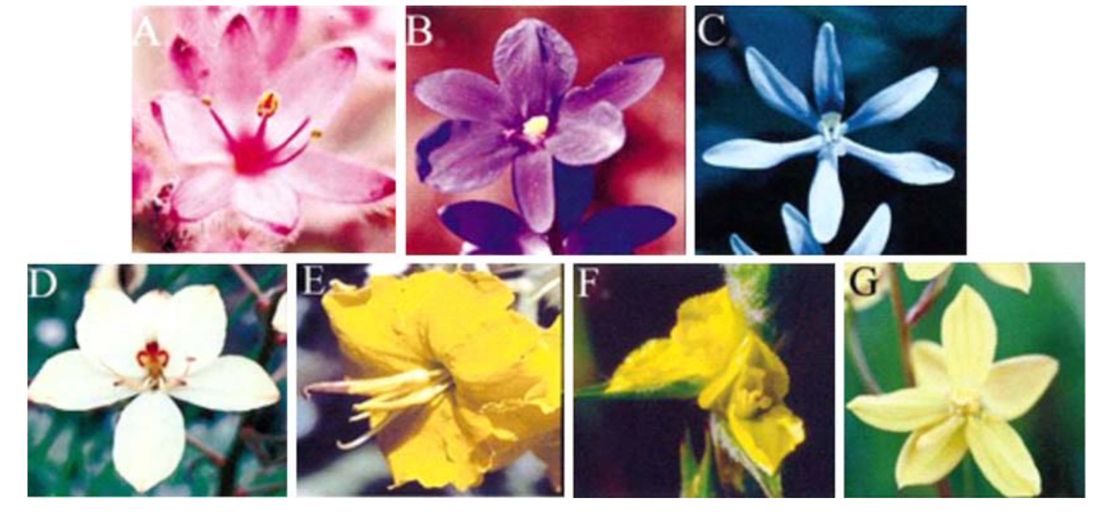


图3 镜像花柱植物成熟花的结构(引自Jesson & Barrett, 2003)。**A.** *Dilatris corymbosa* (Haemodoraceae)。**B.** *Monochoria australasica* (雨久花科)。**C.** *Heteranthera limosa* (雨久花科)。**D.** *Wachendorfia paniculata* (Haemodoraceae)。**E.** 黄花刺茄 (茄科)。**F.** 田葱 (田葱科)。**G.** *Cyanella lutea* (异蕊草科)。

Fig. 3. Mature flower structure of enantiostylous plants (from Jesson & Barrett, 2003). **A,** *Dilatris corymbosa* (Haemodoraceae). **B,** *Monochoria australasica* (Pontederiaceae). **C,** *Heteranthera limosa* (Pontederiaceae). **D,** *Wachendorfia paniculata* (Haemodoraceae). **E,** *Solanum rostratum* (Solanaceae). **F,** *Philydrum lanuginosum* (Philydraceae). **G,** *Cyanella lutea* (Tecophilaeaceae).

倍以上，但传粉花药和喂饲花药的花粉败育率无差异(Bowers, 1975; 高芳等, 2005)。二型镜像花柱植物*C. alba*传粉花药中的花粉数多于每一枚喂饲花药的花粉数(Dulberger & Ornduff, 1980)。

从雄蕊群与花柱间的关系看，雄蕊异长不是镜像花柱的相关特征，不同类群镜像花柱植物雄蕊群和花柱间的相关排列具有差异。如单型镜像花柱植物非洲紫罗兰的雄蕊大小相同，雄蕊群和花柱着生位置无相关性，而在二型镜像花柱植物*W. brachyandra* Barker、*W. paniculata*、*W. thyrsiflora* L.和*H. multiflora*中，雄蕊群和花柱着生位置在一定程度上表现为相关异型花(Jesson et al., 2003b)。*Wachendorfia* Burm.中的雄蕊群与花柱着生位置存在相关排列，但花药的大小相同，没有雄蕊异长现象；而*Heteranthera* Ruiz & Pav.属的花柱与传粉雄蕊的着生位置相关性较弱，但花内具明显的雄蕊异长现象。因此，虽然花柱与雄蕊着生位置的相关排列是大多数镜像花柱植物，尤其是二型镜像花柱植物的一个重要特征，但这并不足以很好地说明花柱多态现象(Graham & Barrett, 1995)。

从花柱特征看，镜像花柱植物异型花间花柱的大小、颜色均相同，但偏转方向相反，同型花间花柱无差异。单型镜像花柱植物是在同一花序上同时具有左、右花柱花或在同一植株上同时具有左、右花柱花序；而二型镜像花柱植物是在同一居群内同时具有左、右花柱植株(Knuth, 1906; Barrett et al., 2000)。

2 镜像花柱植物在被子植物中的分布及其遗传演化

2.1 镜像花柱植物在被子植物中的分布

从已有文献看，镜像花柱植物已在被子植物的雨久花科等11个科的部分种类中进行

了报道(附录2)。但它们在被子植物中的分布没有明显的规律, 在双子叶和单子叶植物中均有分布。其中单型镜像花柱在单子叶和双子叶植物的一些科中均存在, 而二型镜像花柱仅在单子叶植物雨久花科等3个科的7个种中存在; 非雌雄互补单型镜像花柱存在于龙胆科Gentianaceae、鸭跖草科Commelinaceae、苦苣苔科和雨久花科的部分种类中, 而雌雄互补镜像花柱除了在龙胆科和鸭跖草科中无分布外, 在其余已报道的9个科中均有分布。

2.2 镜像花柱植物的遗传特性与系统演化

Barrett等(2000)认为, 二型镜像花柱与异长花柱(heterostyly)和柱高二态(stigma-height dimorphism)现象一样, 可能也是由孟德尔遗传定律控制的。在受遗传控制并进行异型交配(disassortative mating)的多型花柱自然居群中, 不同花柱类型的植株数目比为1:1 (Barrett, 1992; 张大勇, 2004)。如在以异交为主的二型镜像花柱植物*W. paniculata*自然居群中, 左、右花柱植株的数目相当, 说明其镜像花柱是受遗传控制的(Jesson & Barrett, 2002b); 而对二型镜像花柱植物*H. multiflora*亲代与子代花型的比例研究表明, 其花柱的左、右偏向受单位点控制: 控制右花柱的等位基因R位于控制左花柱的基因r的上位, 进一步证明了二型镜像花柱是由孟德尔遗传定律控制的(Jesson & Barrett, 2002a, b)。

目前, 对具镜像花柱植物的系统演化研究主要集中在同时有单型和二型镜像花柱发生的Haemodoraceae科、雨久花科的*Heteranthera*以及异蕊草科Tecophilaeaceae的*Cyanella* L.等少数类群中。如对Haemodoraceae科的系统发育研究表明, 具二型镜像花柱的类群可能是由具单型镜像花柱的类群进化而来的(Simpson, 1990); 而在雨久花科和茄科植物中, 具单型镜像花柱的类群可能是由具直立花柱的类群进化而来的(Graham & Barrett, 1995; Olmstead & Palmer, 1997)。异蕊草科的*C. lutea*具单型镜像花柱, 而*C. alba*的二型镜像花柱在不同环境中是不固定的(Dulberger & Ornduff, 1980), 据此, Barrett等(2000)认为*C. alba*的二型镜像花柱可能是由单型镜像花柱进化而来。从维持机制看, Barrett等(2000)及Jesson和Barrett (2002a, b)认为直立花柱植物中的所有花都可相互接受和传输花粉, 自交水平较高; 而单型镜像花柱植物中同型花间的花粉传输相对降低(降低的程度取决于植株上左、右花柱花的比例), 自交水平大大降低, 所以得以选择保留。从进化路径看, 单型镜像花柱先由仅具花柱偏转的突变株渗入直立花柱居群, 即花柱偏转的进化, 接着是对花柱和雄蕊着生位置的选择, 即与促进异花花粉准确传输有关的雄蕊的进化; 而二型镜像花柱先由花柱固定偏向一侧的突变株(即左或右花柱突变株)渗入单型镜像花柱居群, 接着是左、右花柱突变株同时渗入, 或通过对单型镜像花柱植株上左、右花柱花的比例分别进行选择而产生二型镜像花柱; 花柱和雄蕊偏转方向相反的突变株不能渗入直立花柱居群(Jesson et al., 2003a)。这些观点均说明单型镜像花柱可能是由直立花柱进化而来, 而二型镜像花柱可能是由单型镜像花柱进化而来。

从单型和二型镜像花柱植物在被子植物中的分布看, 二型镜像花柱植物的数量明显较少。这是因为存在着2种维持单型镜像花柱的选择压力, 分别为: (1)具两种花型的单型镜像花柱植株比二型镜像花柱植株将更能产生繁殖保障(reproductive assurance)效应、提高雌性适合度, 或产生自动选择优势(automatic selection advantage)而提高雄性适合度。(2)镜像花柱植物的遗传特点。如在温室中, 单型镜像花柱植物*M. korsakowii*、*H. mexicana*

Watson和黄花刺茄的绝大多数植株都产生数量近相等的左、右花柱花，说明它们的花柱取向在数量上的可遗传变异极少，而花柱方向可遗传变异的缺乏将极大地抑制对完全为左或右花柱花的花型选择，从而导致单型镜像花柱到二型镜像花柱的进化较少发生(Barrett et al., 2000; 张大勇, 2004)。

3 镜像花的交配式样、传粉特性及其进化生物学意义

3.1 镜像花柱植物的交配式样和交配频率

具镜像花柱的植物均存在一定程度的自交亲和。如二型镜像花柱植物*W. parviflora* W. F. Barker和*W. brachyandra*均具较强的自交亲和能力，植株既可自交也可异交(Jesson & Barrett, 2002c)，而*W. thyrsiflora*、*W. paniculata*和*C. alba*的自交亲和能力较弱，主要进行昆虫介导的异交授粉(Ornduff & Dulberger, 1978; Dulberger & Ornduff, 1980; Jesson & Barrett, 2002c)，且*W. paniculata*右花柱花间的自交亲和性强于左花柱花间的，花型间的亲和性强于花型内的(Ornduff & Dulberger, 1978)。单型镜像花柱植物*C. fasciculata*、黄花刺茄、耳叶决明*Cassia auriculata* L.、复总望江南、*M. korsakowii*、*M. vaginalis*和淡褐蛛毛苣苔*Paraboea rufescens* (Franch.) Burtt的自交亲和能力通常较弱，主要进行昆虫介导的异交授粉(Hardin et al., 1972; Bowers, 1975; Dulberger, 1981; Tang & Huang, 2005; Gao et al., 2006)；黄花刺茄和淡褐蛛毛苣苔同株异花的受精水平和异株异花受精水平还依赖于植株上开花数目的多少和传粉者的飞行式样(Bowers, 1975; Gao et al., 2006)。这些结果说明：镜像花柱植物虽然具有促进异交的花部特征，但均具有自交、异交和混合式交配等多重式样，且这些式样与镜像花柱的类型没有必然的联系，不同镜像花柱植物的交配式样各有其特点。

镜像花柱植物的交配频率也复杂多样。在人工授粉条件下，二型镜像花柱植物*W. paniculata*的结实率在Vredehoek居群中表现为花型间大于花型内，在Camps Bay居群中则无显著差异；在*W. thyrsiflora*中，自花授粉、花型内和花型间各种授粉处理的结实率均无显著差异(Jesson & Barrett, 2002c)。单型镜像花柱植物黄花刺茄自花授粉、花型内和花型间各种授粉处理的结实率均无显著差异，但自然传粉结实率明显高于人工授粉的(Bowers, 1975)；淡褐蛛毛苣苔的结实率表现为花型内授粉>花型间授粉>自然授粉(Gao et al., 2006)。从结籽量看，二型镜像花柱植物*W. paniculata*、*W. brachyandra*和*W. thyrsiflora*花型内和花型间授粉处理后每果实的结籽量均无显著差异(Jesson & Barrett, 2002c)；而在已报道的单型镜像花柱植物中，除淡褐蛛毛苣苔外，*C. fasciculata*、耳叶决明、复总望江南和黄花刺茄均表现为植株自交亲和能力越强，自交后每果实产生的种子数越多(Bowers, 1975; Ornduff & Dulberger, 1978; Dulberger & Ornduff, 1980; Jesson & Barrett, 2002c; Gao et al., 2006)，这与Cruden和Lyon (1985)以及Lloyd (1987)的报道类似。Jesson和Barrett (2002b)将黄花刺茄花中的花柱模拟成二型镜像花柱、单型镜像花柱和直立花柱，对其交配频率的检测表明：各种处理间的异交率表现为二型镜像花柱(异交率为0.9)>单型镜像花柱(异交率为0.75)>直立花柱(异交率为0.35)，且在二型镜像花柱的处理中，大部分交配事件发生于花型间；各种处理的同株异花受精水平表现为二型镜像花柱<单型镜

像花柱<直立花柱。综合上述结果可以看出，植物在从直立花柱向二型镜像花柱的进化过程中其异交率不断增加，表明镜像花柱植物的镜像花是通过减少同株异花受精的花粉传输来促进有效的异株间花粉传输，但为什么镜像花柱植物在不同居群、甚至在自花授粉及花型内和花型间各种授粉处理时的结实率和结籽量会表现出不同程度的差异？究竟有哪些选择压力导致了这些差异的产生？这些差异在镜像花柱植物的进化中具有哪些意义？这些问题都是镜像花柱植物交配系统研究中的核心问题，也是镜像花研究中的一个焦点和难点问题。

3.2 镜像花的传粉特点

从已有的报道看，大多数镜像花柱植物的镜像花通常具有一些共有的相关特征，表现为: (1)花无花蜜，喂饲雄蕊偏上，传粉雄蕊偏下; (2)花药以孔裂方式开裂; (3)雄蕊偏转导致喂饲花药的花粉沉积于传粉昆虫身体中部，传粉花药的花粉沉积于昆虫身体侧面或后面; (4)柱头微小; (5)柱头接触已沉积传粉花药花粉的区域等(Dulberger, 1981; Jesson et al , 2003b)。

大多数镜像花柱植物在传粉媒介、访花行为以及给予传粉媒介的酬物上具有相似性。从传粉媒介看，一些镜像花柱植物具有相同的传粉者，如 *Bombus* spp.是黄花刺茄、*C. fasciculata* 和淡褐蛛毛苣苔的主要传粉者; *Xylocopa* spp.是黄花刺茄、复总望江南和耳叶决明的主要传粉者; *Anthophorids* spp.是 *C. fasciculata* 和黄花刺茄的主要传粉者; *Apis mellifera* 是 *W. thyrsiflora*、*W. brachyandra* 和 *W. paniculata* 的主要传粉者(Harris & Kuchs, 1902; Bowers, 1975; Dulberger, 1981; Fenster, 1995; Jesson & Barrett, 2002c; Gao et al., 2006)。从访花行为看: 传粉者对花的访问是随机的，但通常只访问当天新开放的花，在每朵花上的访问持续时间为 1–3 s; 传粉者采集花粉时，将身体卷曲朝向喂饲雄蕊顶端，并用大颚抓住喂饲雄蕊基部，向传粉雄蕊尖端位置边振动翅膀边吸取喂饲雄蕊花药中的花粉。此过程是伴随它们发出的较大嗡嗡声进行的。传粉者在将采集到的喂饲花药的花粉释放到腹部的同时，传粉花药接触到其翅膀下身体的一侧，柱头则接触到相应的另一侧(Bowers, 1975; Thorp & Estes, 1975; Lee & Bazzaz, 1982; Fenster, 1991; Dulberger, 1981; Gao et al., 2006)。从给予传粉媒介的酬物看，大多数镜像花柱植物主要以花粉作为传粉媒介的酬物，只有二型镜像花柱植物 *W. paniculata* 以花蜜作为酬物(Ornduff, 1974; Ornduff & Dulberger, 1978)。

3.3 镜像花柱的进化生物学意义

3.3.1 保护功能型雄蕊和雌蕊 镜像花柱常常与异型雄蕊相联系(Dulberger, 1981; Jesson et al., 2003a)。很多镜像花柱植物的异型雄蕊不仅在形态、大小上不同，花药(有时包括花丝)的颜色往往也不同(Jesson & Barrett, 2003)。喂饲花药通常具有比较鲜艳的色彩，且与花冠(花被)的颜色形成鲜明对比，易引起传粉者注意；而传粉花药的颜色大多比较暗淡，不易被访花昆虫发现(Müller, 1883; Nepi et al., 2003)，从而可保护用于繁殖的功能型花粉不被昆虫吃掉(Renner, 1989)。从镜像花柱的形态看，它可使昆虫接近喂饲雄蕊，从而避免昆虫振动损伤雌性器官；雌蕊偏离花对称轴，柱头接触传粉者身体的后部或侧面而不是腹部，使其更不可能受到损伤(Dulberger, 1981)。

3.3.2 产生繁殖保障效应 镜像花柱植物的自交亲和特性使植株在早春温度较低、生境

条件较为恶劣或种群密度较低等因素导致传粉者作用受限制而致外来花粉量不足的情况下，可产生繁殖保障效应(Barrett, 2002b)。如二型镜像花柱植物*W. brachyandra*和*W. parviflora*均具较强的自交亲和能力，*W. brachyandra*还具延迟自交特性，它们均可在传粉者限制的情况下通过自交来提高结实率以保障繁殖成功(Jesson & Barrett, 2002c)；在美国俄克拉荷马州，自交亲和的黄花刺茄较大居群的异株异花受精较为频繁，较小居群由于受传粉者限制而同株异花受精的自交较为频繁，以此产生繁殖保障效应来提高个体植株的适合度(Bowers, 1975)。

3.3.3 促进有效的异花粉传输，提高异交率和雄性适合度 在镜像花柱植物中，镜像花通常无花蜜、具异型雄蕊，这些相关特征使其主要以花粉作为传粉媒介的报酬，镜像花柱通过使花柱偏离传粉者的访花路径来减小柱头和花药间的相互干扰、使花粉分布在传粉者身体的不同侧面，只有左、右花柱花间才能进行授粉，避免同一花型间的交配，促进异型花间的异花粉传输，有效地提高异交率((Jesson & Barrett, 2003; 张大勇, 2004)。如在具单型镜像花柱的*C. lutea*和具二型镜像花柱的*C. alba*中，花内只有1枚起传粉作用的雄蕊，它的弯曲方向与花柱弯曲方向相反，左花柱花的雄蕊弯向右侧，右花柱花的雄蕊弯向左侧(Dulberger & Ornduff, 1980; Dulberger, 1981)；单型镜像花柱植物黄花刺茄的1枚雄蕊长于其他4枚，顶端弯曲偏向一侧，花柱与其近等长但弯向另一侧(Todd, 1882; Bowers, 1975; Hawkes et al., 1979)，柱头只能接收到昆虫身体相应一侧所携带的花粉。因此，只有访问过右花柱花的昆虫才可使左花柱花授粉，反之亦然。Jesson和Barrett (2002a, b, 2005)采用模拟花和花序的方法，将黄花刺茄的花柱分别处理为二型镜像花柱、单型镜像花柱、直立花柱、完全左花柱和完全右花柱5种情况，并采用水平淀粉凝胶电泳方法对其交配式样和雌性生育力进行了分析。结果表明，镜像花柱显著提高了异交率，且各处理间的异交率表现为二型镜像花柱或完全左花柱或完全右花柱>单型镜像花柱>直立花柱，二型镜像花柱和完全左花柱或完全右花柱间的异交率无显著差异。二型镜像花柱比单型镜像花柱异交率高但同株异花受精水平低，单型镜像花柱比直立花柱异交率高但同株异花受精水平低。这些结果说明与直立花柱相比，二型镜像花柱和单型镜像花柱都是通过减少同株异花受精的花粉传输来促进有效的异花粉传输。Gao等(2006)对淡褐蛛毛苣苔的观察也得到了相似的结论。由此可见，镜像花柱植物的花柱多态现象是一种更趋向于促进花型间异花粉传输、提高异交率和雄性适合度的花部特征(Todd, 1882; Bowers, 1975; Ornduff & Dulberger, 1978; Fenster, 1995; Jesson & Barrett, 2002b, 2003)。

二型镜像花柱植物的大部分异交事件发生在花型相反的植株间，各处理间的雌性生育力无显著差异；但在花粉限制情况下，二型镜像花柱和单型镜像花柱的雌性生育力显著高于完全左花柱花或完全右花柱花的雌性生育力，说明镜像花柱的进化是为了减小自交强度、促进相反花型间的花粉传输、提高植株的雄性适合度(Jesson et al., 2003a; Jesson & Barrett, 2005)。另外，一般较大的花展示对雄性功能尤其有利，因为同时开放许多花的花序可以吸引更多的昆虫访问，输出更多的花粉(张大勇, 2004)。大多数镜像花柱植物具有较大的花展示(Jesson & Barrett, 2002a)，再加上其具有特殊偏转的镜像花柱，这些镜像花特征更有利于用于异交的花粉输出，从而明显地提高雄性适合度(Jesson et al., 2003a)。

4 展望

镜像花柱作为被子植物的一种花柱多态现象，以其在研究繁育系统进化上的重要价值受到了国内外越来越多的植物进化生物学家的关注(Jesson & Barrett, 2002a, b, 2003; 2005; Tang & Huang, 2005; Gao et al., 2006)。但从研究的范围和内容看，上述研究还仅限于对少数镜像花植物不同层次繁育特性的观察，无法从广度和深度上全面揭示镜像花柱在被子植物繁育系统进化中的意义。我们认为，今后还应在扩大研究类群的基础上，从以下几个方面对该现象进行深入系统的研究:

(1) 在自然条件及实验控制条件下，对镜像花中镜像花柱与异型雄蕊的关系、异型雄蕊的分工及其传粉特性进行深入研究，以探讨它们与传粉者之间的协同进化关系以及在提高植物雄性适合度方面的意义。

(2)在形态、等位酶及分子水平上，进一步对镜像花柱植物的交配系统，尤其是镜像花型内和型间的交配频率等进行研究，以揭示镜像花的花部特征在避免同一花型间的交配、提高异交率等方面的进化意义。

(3)从进化发育生物学(Evo-Devo)角度，对镜像花柱与异型雄蕊的发生、发育进行深入研究，探讨镜像花表型起源和进化的分子机制，并由此揭示镜像花基因型与表型之间的关系。

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附录1 镜像花雄蕊群的特征
Appendix 1 Stamen characteristics of enantiostyly

类群 Taxa	雄蕊数目 Number of stamen	雄蕊着生位置与形态 Position and morph of stamen	雄蕊偏向 Deflection of stamen	参考文献 References
单型镜像花柱 Monomorphic enantiostyly				
耳叶决明 *Cassia auriculata* L.	雄蕊10枚，不育雄蕊3枚，可育雄蕊7枚，包括3枚传粉雄蕊和4枚喂饲雄蕊 10 stamens, including 3 sterile stamens and 7 fertile stamens. Fertile stamens include 3 pollinating stamens and 4 feeding stamens.	不育雄蕊位于花最上部，短而粗、黄色的喂饲雄蕊位于花中部，2枚较大的深褐色传粉雄蕊位于喂饲雄蕊下方，在花最底部2枚传粉雄蕊间着生另一枚发生弯曲的深褐色传粉雄蕊 Sterile stamens are located at the uppermost position. Short and thick and yellow feeding stamens are arranged in the center position, below which there is a pair of 2 large and dark brown pollinating stamens. Between these 2 stamens is located a lowermost dark brown pollinating stamen.	2枚传粉雄蕊与花柱偏向相同，另一枚传粉雄蕊与花柱偏向相反，喂饲雄蕊不发生偏转 2 pollinating stamens are deflected uniform to the style, and the other is deflected opposite to the style; feeding stamen does not deflect.	Dulberger, 1981
复总望江南 *C. didymobotrya* Fresen.	同上，但可育雄蕊包括2枚传粉雄蕊和5枚喂饲雄蕊 Idem, but fertile stamens contain 2 pollinating stamens and 5 feeding stamens.	同上，但在花最底部两枚传粉雄蕊间着生着另一枚深褐色不发生偏转的喂饲雄蕊 Idem, but the single lowermost dark brown stamen does not deflect and is feeding stamen.	2枚传粉雄蕊中1枚偏左，另一枚偏右，喂饲雄蕊不发生偏转 1 pollinating stamen is deflected uniform to the style, and the other opposite to the style; feeding stamen does not deflect.	

附录1 (续) **Appendix 1** (continued)

类群 Taxa	雄蕊数目 Number of stamen	雄蕊着生位置与形态 Position and morph of stamen	雄蕊偏向 Deflection of stamen	参考文献 References
Chamaecrista fasciculata (Michx.) Greene	雄蕊10枚，二体，无传粉雄蕊和喂饲雄蕊的分化 10 diadelphous stamens without division of pollinating stamen and feeding stamen.	雄蕊大小无明显差异，花丝联合的9枚雄蕊位于花上部，上有帽状花瓣，单雄蕊位于花底部 Size of 10 stamens is similar. 9 of them have united filaments located at the upper position that are covered with a rigid upper cucullus petal, and the other one is located at the lower position.	花丝联合的雄蕊弯曲并偏离花柱，单雄蕊与花柱平行 9 stamens with united filament curved away from style. The tenth stamen is parallel to the style.	Todd, 1882; Fenster, 1995
Cyanella lutea L. f.	雄蕊6枚，传粉雄蕊1枚，喂饲雄蕊5枚 6 stamens, including 1 pollinating stamen and 5 feeding stamens.	雄蕊黄色，传粉雄蕊长于喂饲雄蕊且较宽，与花瓣相邻位于花底部，喂饲雄蕊彼此相邻位于花上部 Stamens are yellow. Longer and broader pollinating stamen is located at the base of flower and adjacent to petal. Feeding stamens are located upper and adjacent to each other.	传粉雄蕊与花柱偏向相反，喂饲雄蕊向花中心内弯 Pollinating stamen is deflected opposite to the style, and feeding stamens are recurved to center of flower.	Dulberger & Ornduff, 1980; Jesson et al., 2003b
Dilatris corymbosa Bergius	雄蕊3枚，传粉雄蕊2枚，喂饲雄蕊1枚 3 stamens, including 2 pollinating stamens and 1 feeding stamen.	较大的黑色传粉雄蕊和较小的橙色喂饲雄蕊与花瓣相邻远离花轴 2 larger dark pollinating stamens and 1 smaller feeding stamen are always adjacent to the tepal and furthest away from the floral axis.	1枚传粉雄蕊与花柱偏向相同，另一枚传粉雄蕊与花柱偏向相反，喂饲雄蕊不发生偏转 1 pollinating stamen is deflected uniform to the style, and the other opposite to the style; feeding stamen does not deflect.	Jesson et al., 2003b
Heteranthera mexicana Watson *H. rotundifolia* Griseb. *H. limosa* Willd.	雄蕊3枚，传粉雄蕊1枚，喂饲雄蕊2枚 3 stamens, including 1 pollinating stamen and 2 feeding stamens.	较大的蓝紫色传粉雄蕊位于花底部与花瓣相邻，较小的黄色喂饲雄蕊位于花中央 The larger purple-blue pollinating stamen is located at the lower position adjacent to the tepal. Smaller yellow feeding stamens are located at the center position.	传粉雄蕊与花柱偏向相反，喂饲雄蕊不发生偏转 Pollinating stamen is deflected opposite to the style, and feeding stamens do not deflect.	Jesson et al., 2003b
Monochoria australasica Ridl.	雄蕊6枚，无传粉雄蕊和喂饲雄蕊的分化 6 stamens, without the division of pollinating stamen and feeding stamen.	雄蕊均为黄色，大小无差异，以顺时针或逆时针方向螺旋状排列于花中央 6 yellow stamens with similar size are arranged in a spiral pattern in either clockwise or counterclockwise in the flower.	均不发生偏转 No stamens are deflected.	Jesson et al., 2003b
M. korsakowii Regel & Maack *M. vaginalis* (Burm. Fil.) Kunth	雄蕊6枚，传粉雄蕊1枚，喂饲雄蕊5枚 6 stamens, including 1 pollinating stamen and 5 feeding stamens.	较大的黑色传粉雄蕊与黄色喂饲雄蕊呈圆锥状排列于花中央 The larger dark pollinating stamen and yellow feeding stamens are arranged conically in the center position of the flower.	传粉雄蕊与花柱偏向相反，喂饲雄蕊不发生偏转 Pollinating stamen is deflected opposite to style, but feeding stamens do not deflect.	Wang et al., 1995; Jesson et al., 2003b, Tang & Huang, 2005
田葱 *Philydrum lanuginosum* Gaertn.	雄蕊1枚，无传粉雄蕊与喂饲雄蕊的分化 1 stamen, without division of pollinating stamen and feeding stamen.	雄蕊黄色，位于花底部，与花瓣相邻 Yellow stamen is located at the lower position adjacent to the tepal in the flower.	均不发生偏转 No stamens are deflected.	Jesson et al., 2003b
淡褐蛛毛苣苔 *Paraboea rufescens* (Franch.) Burtt	雄蕊4枚，传粉雄蕊和喂饲雄蕊各2枚 4 stamens, including 2 pollinating stamens and 2 feeding stamens.	白色传粉雄蕊与黄色喂饲雄蕊大小相同，位于花中央，偏离花柱 White pollinating stamens and yellow feeding stamens are located at the center of the flower and deflected away from the style.	传粉雄蕊与喂饲雄蕊粘在一起与花柱偏向相反 Pollinating stamens and feeding stamens are cohesive and deflected opposite to the style.	Gao et al., 2006

附录1 (续) **Appendix 1** (continued)

类群 Taxa	雄蕊数目 Number of stamen	雄蕊着生位置与形态 Position and morph of stamen	雄蕊偏向 Deflection of stamen	参考文献 References
黄花刺茄 *Solanum rostratum* Dunal.	雄蕊5枚，传粉雄蕊1枚，喂饲雄蕊4枚 5 stamens, including 1 pollinating stamen and 4 feeding stamens.	较大的黄色但尖端暗绿色或紫色的传粉雄蕊位于花底部与花冠融合，较小的鲜黄色喂饲雄蕊圆锥状排列于花中央 Dark yellow or brown pollinating stamen is fused to the corolla in a lower position. Bright yellow feeding stamens are arranged conically in the center position of the flower.	传粉雄蕊与花柱偏向相反，喂饲雄蕊不发生偏转 Pollinating stamen is deflected opposite to the style, but feeding stamens are not deflected.	Todd, 1882; Bowers, 1975
二型镜像花柱 Dimorphic enantiostyly				
Cyanella alba L. f.	雄蕊6枚，传粉雄蕊1枚，喂饲雄蕊5枚 6 stamens, including 1 pollinating stamen and 5 feeding stamens.	雄蕊均为黑黄色，大小无差异，但传粉雄蕊相对扁平且较宽位于花底部，喂饲雄蕊花药联合位于花上部 Size of 6 dark yellow stamens is similar. The pollinating stamen is flattened and broader than feeding stamen and located at the lower position. 5 feeding stamens are fused and located at the upper position.	传粉雄蕊与花柱偏向相反，喂饲雄蕊向花中心内弯 Pollinating stamen is deflected opposite to the style, and feeding stamens are recurved at the center position of the flower.	Dulberger & Ornduff, 1980
Heteranthera multiflora (Griseb.) Horn	雄蕊3枚，传粉雄蕊1枚，喂饲雄蕊2枚 3 stamens, including 1 pollinating stamen and 2 feeding stamens.	较大的蓝紫色传粉雄蕊位于花底部与花瓣相邻，较小的黄色喂饲雄蕊位于花中央 The larger purple-blue pollinating stamen is located at the lower position adjacent to the tepal, and the smaller feeding stamens are located at the center position.	传粉雄蕊与花柱偏向相反，喂饲雄蕊不发生偏转 Pollinating stamen is deflected opposite to the style, and feeding stamens are not deflected.	Jesson et al., 2003b
Wachendorfia paniculata L.	雄蕊3枚，无传粉雄蕊和喂饲雄蕊的分化 3 stamens, without division of pollinating stamen and feeding stamen.	雄蕊均为黄褐色，大小无差异, 2枚雄蕊位于花上部，位于花底部的1枚雄蕊高度与柱头的高度相同并高于上部2枚雄蕊的高度 Size of 3 brown-yellow stamens is similar. 2 stamens are located at the upper position, and the third stamen is located at the lower position of the flower. The stigma and the third stamen are equal in height but higher than the other two stamens.	位于花上部2枚雄蕊中的一枚与花柱偏向相同，另一枚与花柱偏向相反，位于花底部的第3枚雄蕊与花柱偏向相反 1 of 2 upper stamens is deflected uniform to the style, and the other is deflected opposite to the style. The third lower stamen is deflected opposite to the style.	Ornduff & Dulberger, 1978; Jesson & Barrett, 2002c

附录2 镜像花柱植物在被子植物中的分布
Appendix 2 The distribution of enantiostyly in angiosperms

分类群 Taxa	镜像花柱类型[1)] Type of enantiostyly[1)]	文献 References
双子叶植物 Dicotyledons		
1 Cyanastraceae	ME or RE	Dulberger & Ornduff, 1980; Fenster, 1995
2 豆科(Leguminosae)		
复总望江南*Cassia didymobotrya* Fresen. 耳叶决明*C. auriculata* L., *C. marilandica* L.	ME or RE	Müller, 1883; Dulberger & Ornduff, 1979; Bir Bahadur et al., 1979; Meehan, 1886; Robertson, 1890
Chamaecrista fasciculata (Michx.) Greene	ME or RE	Todd, 1882; Dulberger, 1981; Irwin & Barneby, 1982
3 紫茉莉科Nyctaginaceae	ME or RE	Webb & Lloyd, 1986; Fenster, 1995
4 苦苣苔科Gesneriaceae		
淡褐蛛毛苣苔*Paraboea rufescens* (Franch.) Burtt	ME or RE	Gao et al., 2006
非洲紫罗兰*Saintpaulia ionantha* Wendl.	ME or NRE	Harrison et al., 1999
扭果苣苔属*Streptocarpus* Lindl.	ME or RE	Harrison et al., 1999
5 龙胆科Gentianaceae		
藻百年属*Exacum* L.	ME or NRE	Lloyd & Webb, 1992
6 茄科Solanaceae		
Solanum citrullifolium A. Br.	ME or RE	Bowers, 1975
黄花刺茄*S. rostratum* Dunal.	ME or RE	Todd, 1882; Bowers, 1975

附录2 (续) **Appendix 2** (continued)

分类群 Taxa	镜像花柱类型[1)] Type of enantiostyly[1)]	文献 References
单子叶植物 Monocotyledons		
7 鸭跖草科Commelinaceae		
穿鞘花属*Amischotolype* Hassk.		
Coleotrype Clarke	ME or NRE	Evans et al., 2000
Murdannia Royle		
Porandra Hong		
8 Haemodoraceae		
Barberetta aurea Harv.	DE or RE	Ornduff, 1974; Ornduff & Dulburger, 1978
Dilatris corymbosa Bergius	ME or RE	Ornduff & Dulburger, 1978; Simpson, 1990
D. viscose L. f.	ME or RE	Jesson & Barrett, 2003
Haemodorum Sm.	ME or RE	Jesson & Barrett, 2002a
Lachnanthes Ell.	ME or NRE	Simpson, 1990
Schiekia Meisn.	ME or RE	Simpson, 1990
Wachendorfia brachyandra Barker		
W. paniculata L.	DE or RE	Ornduff, 1974; Ornduff & Dulburger, 1978; Wilson, 1887
W. parviflora W. F. Barker		
W. thyrsiflora L.		
9 田葱科Philydraceae		
田葱*Philydrum lanuginosum* Gaertn.	ME or RE	Simpson, 1990; Graham & Barrett, 1995
10 雨久花科Pontederiaceae		
Heteranthera limosa Willd.	DE or RE	Jesson & Barrett, 2002*b*
H. mexicana Watson		
H. multiflora (Griseb.) Horn	ME or RE	Iyengar, 1923; Graham & Barrett, 1995
H. rotundifolia Griseb.		
Monochoria australasica Ridl.	ME or NRE	Jesson & Barrett, 2003
M. hastata (L.) Solms	ME or RE	Wang et al., 1995; Jesson & Barrett, 2003; Tang & Huang, 2005
M. korsakowii Regel & Maack		
M. vaginalis (Burm. Fil.) Kunth		
11 异蕊草科Tecophilaeaceae		
Cyanella alba L. f.	DE or RE	Ornduff, 1974; Dulberger & Ornduff, 1980
C. lutea L. f.	ME or RE	Ornduff, 1974; Dulberger & Ornduff, 1980

1) ME，单型镜像花柱; DE，二型镜像花柱; RE，雌雄互补镜像花柱; NRE，非雌雄互补镜像花柱。

1) ME, monomorphic enantiostyly; DE, dimorphic enantiostyly; RE, nonreciprocal enantiostyly; NRE, reciprocal enantiostyly.